1 Drought, Stress, and the Origin of Adaptations

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1. INTRODUCTION

Before discussing the modifications or adaptations in structure and function that enable some plants to survive water and high temperature stress better than others, let us review the general mechanism by which environmental stresses affect plant growth. For example, drought causes plant water deficits that reduce cell turgor, causing closure of stomata and reduction in cell enlargement, thereby reducing both the leaf surface area and the rate of photosynthesis per unit of leaf area. If the plant water deficit becomes more severe, the photosynthetic machinery is damaged, further reducing the rate of photosynthesis per unit of leaf area. High temperature increases the rate of water loss and the use of food in respiration. It also sometimes damages the photosynthetic machinery, as pointed out in Chapter 15.

An environmental factor such as water deficit or high temperature, or a change in genotype, can affect plant growth and yield only by affecting the physiological processes and conditions in plants (Figure 1.1). Thus to know why certain species and varieties survive or even thrive in habitats where others fail requires a better understanding of how their physiological processes are affected by various environmental factors. Furthermore, if a plant breeder produces a higher yielding variety, it is because a more efficient

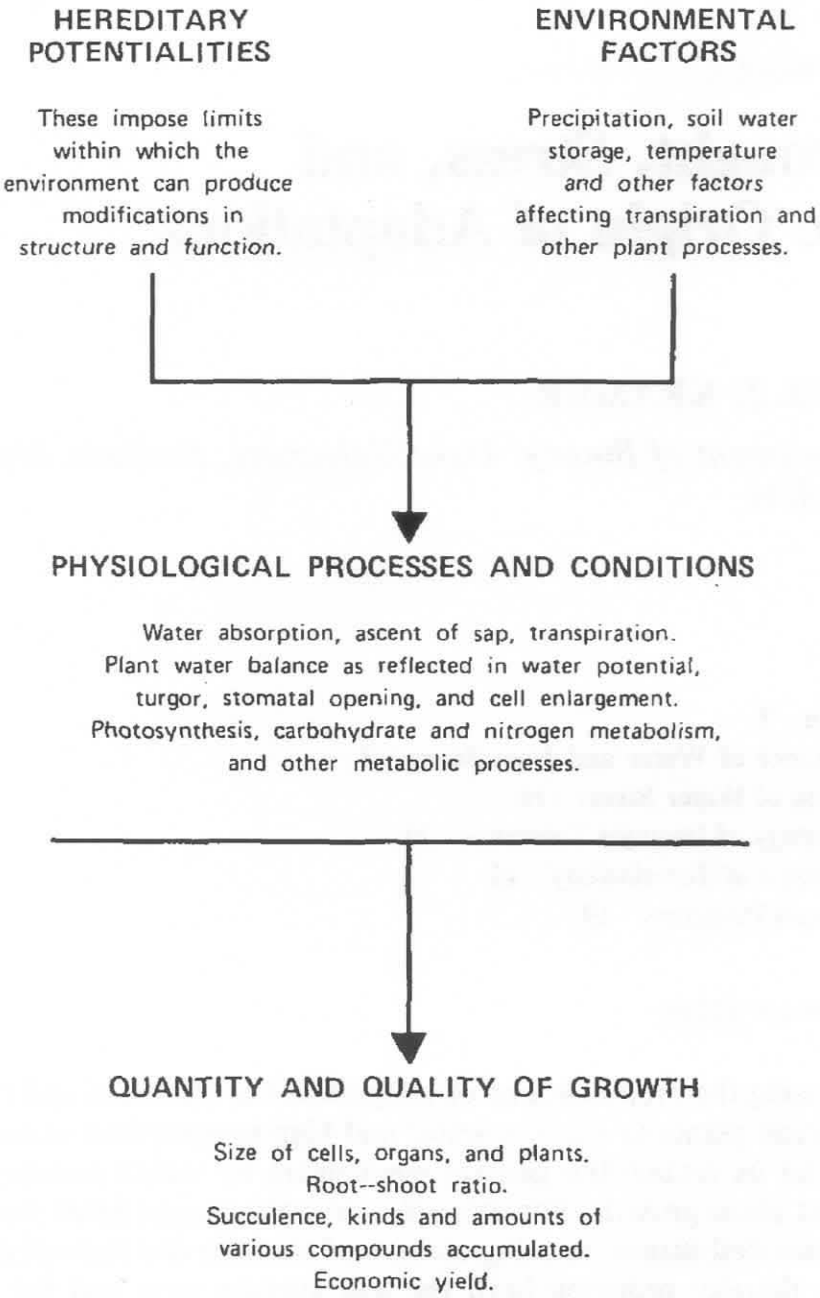

Figure 1.1. How the quantity and quality of plant growth is controlled by an organism's hereditary potentialities and its environment, operating through its physiological processes and conditions.

combination of physiological processes has been arrived at for a particular environment.

2. THE IMPORTANCE OF WATER AND HEAT STRESS

Crop plants rarely attain their full genetic potential for yield because of the limitations imposed by the environment, especially unfavorable tempera-

tures and lack of water. About one-third of the world's potentially arable land suffers from an inadequate supply of water, and on most of the remainder crop yields are periodically reduced by drought. Plant water deficits affect every aspect of plant growth (1) and the worldwide losses in yield from water stress probably exceed the losses from all other causes combined. The importance of water in relation to plant growth is discussed in detail in Part V.

High temperature stress receives less attention than water stress, except in relation to vegetation growing in hot deserts. However the manner in which high temperature affects plants is probably better understood than are some of the effects of water stress.

2.1. Heat Stress

The effects of heat stress are often confounded with those of water stress because drought usually is accompanied by high temperature, which increases the rate of transpiration and hastens the occurrence of injurious dehydration. There also may be depletion of carbohydrates because the maximum rate of respiration usually occurs at a higher temperature than the maximum rate of photosynthesis. Furthermore, the cooling effects of transpiration are reduced in water-stressed plants, resulting in increased leaf temperatures, which decrease apparent photosynthesis and may disturb nitrogen and lipid metabolism and injure cell membranes. Some Soviet investigators claim that ammonia is released at high temperatures, causing injury. Direct heat injury is less common but often occurs to stems of seedlings at the soil surface and to plants in the hottest deserts. The effects of high temperature were reviewed by Levitt (2) and are discussed in more detail in Part IV.

Low Temperature Stress. The extensive research on cold and chilling injury lies outside of the scope of this book. However low soil temperature often reduces water absorption and causes water stress, resulting in injury that sometimes is mistakenly attributed to low temperature. This was observed in cotton by St. John and Christiansen (3, p. 259).

2.2. Temperature Perturbations

There is much discussion concerning the probable effects on plant growth and crop yield of a small increase or decrease in the global temperature. This subject is important in the long term, but of more immediate concern in agriculture are the short periods of abnormally high or low temperatures that often occur during the growing season. There is evidence that a week or less of abnormally high or low temperature can measurably affect growth and yield. For example, Powell and Huffman (4) reported that 6 days at above or below normal temperature during seed development reduces seed size of

sorghum, and Akpan and Bean (5) concluded that year-to-year variations in temperature affect the yield and quality of seed of pasture grasses. It also has been shown that the temperature regime in which the seed was developed affects the growth of tobacco seedlings (6). It therefore seems that more research is needed on the effects of short periods of temperature stress at various stages of growth because these incidents are more immediately important than possible long-term shifts in the world temperature. Fischer (Chapter 21, Section 6.2) also points to effects of short periods of atmospheric stress on seed filling in grain crops and concludes that more research is needed to determine the significance of these stresses.

3. MEASUREMENT OF WATER STRESS

Progress in all branches of science has always depended on the development of new methods and new instrumentation. This was particularly true in the field of plant water relations, where progress was hindered for many years by lack of convenient methods of measuring stress.

The need for quantitative measurements of water stress was appreciated by ecologists and physiologists early in this century, but the only method available was to measure the osmotic potential of expressed sap. This method provided useful information, including evidence of daily and seasonal changes in osmotic potential and a decrease in osmotic potential in plants subjected to water stress (7; 8, pp. 39–45). However by 1940 fewer measurements of osmotic potential were being made. One reason for this was the uncertainty about whether expressed sap provided reliable samples. In addition, it was increasingly appreciated that water movement is controlled by differences in water potential rather than by differences in osmotic potential. Unfortunately, no convenient method of measuring water potential was then available; hence the value of several decades of research on plant water relations was reduced by lack of quantitative measurements of plant water stress.

Usable thermocouple psychrometers became available by 1960, and shortly afterwards the pressure chamber was introduced. Now we can measure the water potential of soil, roots in the soil, and attached leaves, as well as detached leaves and twigs. The availability of equipment for measuring water potential may have led to overemphasis on this variable, which is only one of three terms in the equation for cell and tissue water potential ψ:

$$\psi = \pi + P \tag{1.1}$$

where π = osmotic potential
P = turgor or pressure potential

It is generally agreed that water movement is controlled by the water potential and cell enlargement by the turgor or pressure potential. Now there

is increasing interest in the possibility that reduced turgor is the factor directly affecting metabolic processes in stressed plants (1, p. 563; Chapter 7, this book). Furthermore, there is strong interest in the importance of a decrease in osmotic potential or osmotic adjustment as an adaptive mechanism to water stress (Chapter 7). Thus to fully understand what is occurring in plants subjected to water deficits it is necessary to measure both water potential and osmotic potential and to calculate the turgor potential. Water potential usually is measured by the thermocouple psychrometer or pressure chamber (9, 10). However the validity of measurements of osmotic potential made on frozen tissue or expressed sap is sometimes questioned because of the possibility of dilution by cell wall water. One way of avoiding this error is use of the pressure-volume technique described by Tyree and Hammel (11).

Water content, calculated on either a dry or a fresh weight basis, is an unsatisfactory measure of water stress, but field water content as a percentage of water content at saturation is sometimes useful. This is calculated as follows:

$$\text{relative water content (RWC)} = \frac{\text{fresh weight} - \text{dry weight}}{\text{saturated weight} - \text{dry weight}} \times 100 \quad (1.2)$$

The water saturation deficit (WSD), another expression of the same value, is calculated in another way; that is, WSD = 100 − RWC. It is claimed by some workers that plants tolerant of desiccation show a smaller decrease in water potential for a given decrease in water content than those that are less tolerant (see Ref. 12). Methods of measuring water deficit or RWC are described by Barrs (9) and Slavík (10).

4. THE TERMINOLOGY OF DROUGHT TOLERANCE

Since this book deals with adaptations to water and temperature stress, it is imperative that some of the terms be discussed, and it is particularly important to differentiate between "drought" and "plant water stress."

4.1. Drought

Drought is a meteorological and environmental event (13), defined somewhat loosely as absence of rainfall for a period of time long enough to cause depletion of soil moisture and damage to plants. The length of time without rain that is necessary to cause injury depends on the kind of plant, the water-holding characteristics of the soil in which it is growing, and the atmospheric conditions that affect the rates of evaporation and transpiration. Drought may be permanent, as in desert areas; seasonal, as in areas with well-defined wet and dry seasons; or unpredictable, as in many humid climates. Agricultural drought was defined by Van Bavel and Verlinden (14)

as the condition that exists when there is insufficient water available to a crop. They made this more quantitative by estimating the amount of readily available water stored in the root zone, the average rate of loss by evaporation, and the average replenishment by precipitation during each month of the year. From these data were calculated the probable number of drought days, that is, days when soil moisture might be limiting, for plants growing in soil with various water storage capacities in the root zone.

4.2. Stress

It is difficult to define "stress" precisely. In engineering and the physical sciences, the term is usually defined as the force applied per unit area. For example, pressure on a girder produces strain in it. However in biology stress is usually described more loosely as any factor that disturbs the normal functioning of an organism. Levitt (2, also Chapter 28), attempted to apply the physical terminology to living organisms, but it seems unlikely that plant water "stress" will be replaced by plant water "strain."

In the commonly used terminology, "drought" is an environmental stress of sufficient duration to produce a plant water deficit or stress, which in turn causes disturbance of physiological processes. The degree of plant water stress or deficit depends on the extent to which water potential and cell turgor are reduced below their optimum values. Quantitative measurement of water stress was discussed earlier in this chapter (Section 3).

Although plant water stress always accompanies drought, it may occur in the absence of drought, either because of excessive transpiration or because water absorption is inhibited by cold soil, an excess of salt in the soil solution, deficient aeration, or injury to root systems. Most plants are subjected to transient, midday water deficits in hot, sunny weather, even when growing in moist soil. However this book is concerned primarily with stress periods of longer duration, caused by the decreasing availability of soil moisture.

4.3. Drought Resistance or Tolerance

The term "drought resistance" has long been used with reference to the ability of plants to survive drought. However it is an unsatisfactory and even ambiguous term, which I prefer to replace with "drought tolerance." Although "drought" refers to a meteorological phenomenon, it is sometimes misapplied to plant phenomena. An example of this confusion occurs in the following statement from a recent paper: "Growth drought tolerance, defined as the plant drought that is just sufficient to halt the increase of seedling leaf area, varied among seedlings from about −20 to −40 bars. Growth drought avoidance, defined as the difference between plant drought and the drought of the shoot environment, . . ." (15). These are thoroughly confusing statements, because there is no plant drought, but only plant water stress. Also, how can a drought be confined to the shoot environment?

To avoid this kind of confusion, I propose to classify the adaptations by which plants survive in regions subject to drought in two major categories: drought escape and drought tolerance. I prefer use of "avoidance" rather than "escape" because the former more accurately describes the actual situation, but "escape" is used here to prevent confusion with Levitt's terminology (2), which is used in some chapters of this book. The adaptations contributing to drought tolerance can be subdivided into categories of dehydration postponement and dehydration tolerance.

Drought Escape. Drought escape is characteristic of only a few plants, such as desert ephemerals and some plants growing in areas possessing well-defined wet and dry seasons. Drought-escaping plants complete their life cycle, or at least their reproductive cycle, before the dry season begins and are seldom severely stressed. Early maturity often is important when droughts occur late in the growing season. For example, each day by which wheat in Kansas and Nebraska matures earlier than the Kharkof variety results in an increase in yield of nearly 60 kg/ha (16). In mediterranean climates tolerance of low temperature may be an important adaptation for drought escape because it permits growth to start early enough in the season to ensure completion of the life cycle before water becomes limiting.

Drought Tolerance. It is impossible for plants of humid climates to escape random droughts, which are characteristic of much of the temperate zone, and some of them possess other adaptations that increase their tolerance of drought. These can be classified as those that postpone dehydration and those that increase tolerance of dehydration.

Dehydration Postponement. This occurs by means of morphological or physiological modifications that reduce transpiration or increase absorption. Thick cuticle, leaf rolling, responsive stomata, and deep root systems all increase the ability of plants to endure droughts for considerable periods of time without becoming severely dehydrated. Water storage occurs in a few succulents and other plants with large storage organs, but it is negligible factor in crop plants. Among cultivated crops, only pineapple has the thick cuticle and the stomatal behavior characteristic of succulent plants with crassulacean acid metabolism (CAM), and as a result it has a transpiration ratio much lower than that of any other cultivated crop. Dehydration postponement of many crops and wild plants depends on the efficiency of their root systems, a topic discussed in Chapters 5, 6, and 25.

The value of responsive stomata and large root systems is sometimes questioned. For example, prompt closure of stomata in moderately stressed leaves may be advantageous in regions where droughts are of short duration, but detrimental where droughts last for a long time, since photosynthesis is reduced by cutting off the supply of carbon dioxide before the photosynthetic machinery has been inhibited by water stress. It also has been argued

that a high root resistance is advantageous where plants must live on stored moisture, because if less water is absorbed early in the season, more will be available later when the crop is maturing. Many of these special situations were discussed by Begg and Turner (17).

"Dehydration postponement" is equivalent to the term "drought avoidance" as used by Levitt (2) for plants that maintain a high water potential when exposed to an external water stress. This usage is unfortunate because such plants do not avoid drought; rather, they possess various adaptations that enable them to tolerate it. As stated earlier, drought is a meteorological event, and the only plants to avoid it are those that complete their life cycle before drought occurs.

Dehydration Tolerance. The degree of dehydration without permanent injury varies widely, depending on the process under consideration, the stage of development, the duration of stress, and the kind of plant. Readers are referred to Hsiao (1) and Begg and Turner (17) for detailed discussions of factors affecting the degree of injury caused by dehydration.

The reaction of plants to dehydration can be considered from two standpoints, *survival* and *yield.* Survival of severe dehydration is of greater importance with respect to native vegetation than for crop plants because if crops are severely stressed they usually have little economic value. However dehydration tolerance may be more important in crop plants than generally is supposed, because some plants such as sorghum and western wheat grass can tolerate considerable water stress and recover when a drought ends.

The physiological basis for differences among species in tolerance of dehydration must be sought largely at the molecular level, perhaps chiefly in membrane structure and enzyme activity. For example, the cellular fine structure of maize is injured by water stress more than that of sorghum (18). Vieira da Silva (19) also found that the fine structure of cells of drought susceptible cotton is injured more by water stress than that of drought tolerant types. These and other reports suggest that tolerance of moderate dehydration may be of significance in crop plants.

It should be emphasized that the three categories of adaptation are not mutually exclusive because one kind of plant can possess more than one category of adaptation. For example, some varieties of sorghum exhibit early maturity, and sorghums in general possess extensive root systems and some degree of protoplasmic tolerance of dehydration. One of the major problems in the field of stress physiology is to determine what adaptations or categories of adaptation are most important in respect to the survival of plants of particular kinds in specific habitats.

The concept of water stress tolerance is too broad and general to serve as a good basis for plant breeding. The purpose of this book is to identify some of the specific adaptations to water and heat stress that can be used both in ecology and in plant breeding.

5. OTHER PROBLEMS OF TERMINOLOGY

Discussions of the manner in which plants are adapted to special environmental conditions often contain terminology that is of questionable validity both philosophically and scientifically.

5.1. Strategy

Consider the common misuse of the word "strategy." Misapplication of "strategy" and "tactics" in biology is exemplified by the title of a paper by Harper and Ogden, "The Reproductive Strategy of High Plants" (20). Another paper states, "We may usefully view a plant as an intricate control system in which responses to stress are strategies directed towards achieving certain goals" (21, p. 375). Earlier in the same paper we find: "It is the control of leaf area and morphology which is often the most powerful means a mesophytic plant has of influencing its fate." Since "strategy" refers to a plan of action designed to attain some desired end, this is pure teleology. How does a plant know what it should do when confronted by water stress or some other environmental crisis? Scientists can develop research strategies to solve their problems, but plants cannot develop strategies because they do not possess the power to make intelligent decisions. Although terms such as "strategy" and "tactics" may attract reader attention, they are philosophically objectionable when used with respect to the behavior of plants.

5.2. The Concept of Adaptation

Although the theme of this book is adaptation to stress, the concept of "adaptation" is difficult to define because it is used both with respect to the evolutionary origin of a character and with respect to the contribution of a character to the fitness of an organism to survive in its present environment. We are concerned with the latter usage. We therefore describe adaptations as *heritable* modifications in structures or functions that increase the probability of an organism surviving and reproducing in a particular environment, or both. However it often is difficult to determine whether a particular modification in a character is beneficial (i.e., has adaptive value) in a particular environment. It is tempting to assume that if a modification in a character survives, it must be beneficial; but Williams (22) warned that the presence of a character is not proof that it is currently essential or even beneficial to survival in the environment in which the organism now lives.

It also should be emphasized that success of an organism in a particular environment rarely depends on possession of a single adaptive character. According to Bradshaw (23), fitness or adaptation of an organism to an environment depends on possession of an optimum combination of characters that minimizes the deleterious effects and maximizes the advantageous

effects. Thus plant breeders are faced with the difficult task of producing genotypes with an optimum combination of adaptive characters rather than the simpler task of producing genotypes with a single adaptive character. There may be exceptions to this generalization, however, as when success depends on tolerance of a single factor such as excess aluminum.

"Adaptation" is sometimes used carelessly, in a manner implying that plants and animals can undergo modifications *in order to* become better adapted to an environment. There is an important, but sometimes neglected, difference between stating that plants have acquired adaptations in structure and function that enable them to survive water stress and stating that plants acquire adaptations to survive water stress, as implied in the quotations in Section 5.1. The concept of purposeful adaptation in nature was widely held by theologians and some biologists in the eighteenth and nineteenth centuries. However there is no scientific basis for such a view, and no justification for the teleological terminology that seems to be coming back into use.

During the evolution of the plant kingdom, innumerable modifications in structures and processes have occurred as a result of random mutations and recombinations. Most of these were deleterious and disappeared, but a few were beneficial because they enabled the plants possessing them to survive and reproduce more successfully, and these were preserved by natural selection. As a result, plants growing in increasingly dry habitats accumulated various modifications of characters with adaptive values, such as thick cuticle, extensive root systems, low osmotic potential, and tolerance of dehydration that increased the probability of their survival. However the modifications or adaptations that enable plants to survive droughts and live in dry habitats *did not originate for those purposes*. They originated from random mutations and recombinations that probably occurred in plants growing in both moist and dry habitats, but usually were not preserved in moist habitats because they had no survival value. The fact that a certain kind of modification would be beneficial in a changing environment has no bearing on whether it will appear. Many organisms have become extinct because the modifications that would have enabled them to become adapted to a new set of environmental conditions failed to develop.

5.3. Stability of Adaptive Characters

The expression of all characters is controlled by the interaction of heredity and environment, as shown in Figure 1.1. However some are more responsive to the environment than others. If a character is unresponsive and remains relatively unchanged over a wide range of environments, it is described as lacking in plasticity or as phenotypically constant. Examples are the water storage tissue and thick cuticle of succulents, and the low osmotic potential and dehydration tolerance of many xerophytes. If a character is responsive to the environment, it is regarded as phenotypically flexible or phenotypically plastic. Examples of phenotypic plasticity are the differences between sun and shade leaves, the reversible decrease in os-

motic potential observed in some mesophytes when water stressed (Chapter 7, Section 6.1), and the switch from the C_3 pathway of photosynthesis to CAM carbon metabolism found in some succulents when subjected to water stress (Chapter 10, Section 6).

Various terms have been used to categorize the two extremes in phenotypic plasticity (see Ref. 23). Recently Fischer and Turner (24) proposed to classify characters with low phenotypic plasticity as "constitutive" and those with a high degree of plasticity as "facultative." They regarded these terms as synonymous with the concepts of strategy and tactics used by Harper and Ogden (20). The validity of such a classification seems questionable to me because it suggests qualitative differences in plasticity or flexibility, when in fact there are only differences in degree of plasticity.

5.4. Acclimation

"Acclimation" refers to the *nonheritable* modification of characters caused by exposure of organisms to new climatic conditions, such as warmer, cooler, or drier weather. It depends on the occurrence of temporary phenotypic modifications caused by the changing environment. The extent of acclimation that can occur varies widely, depending on the plasticity of the species. For example, the summer annual *Tidestromia oblongifolia* has a very high optimum temperature for photosynthesis and cannot adjust to a lower temperature. In contrast, the optimum temperature for photosynthesis of the evergreen perennial creosote bush (*Larrea divaricata*), is about 10°C lower in the winter than in summer (Chapter 18, Section 2). *Larrea* likewise undergoes considerable acclimation to water stress, the photosynthetic apparatus of plants grown in Death Valley remaining uninhibited at a level of water stress that severely inhibits photosynthesis of plants grown in a humid environment (25).

The difference between adaptation and acclimation is illustrated by the adaptation of photosynthesis in *Eucalyptus* to the temperatures characteristic of various elevations, on which is superimposed short-term acclimation to seasonal variations in temperature (26).

5.5. Hardening

The process of "hardening" appears to be the equivalent of acclimation, and it also depends on phenotypic modifications. It is generally found that plants that have been subjected to several cycles of mild water stress suffer less injury from drought than do plants not stressed previously. Plants are commonly "hardened" before transplanting by exposure to full sun, by decreased frequency of watering, and even by undercutting and loosening (wrenching) the root systems. These treatments usually result in temporary water stress, reduced leaf size, thicker cuticle, and sometimes a larger root/shoot ratio. There also are evidences of protoplasmic changes, as indicated by the differences in reaction of photosynthesis of previously stressed

and unstressed creosote bush to water stress, mentioned in Section 5.4. Some Soviet physiologists claim that treatment of seed by wetting and redrying before sowing will increase the tolerance of water stress by plants grown from the treated seed (27).

There is an extensive body of literature on the hardening of plants to increase their tolerance of low temperature, but the subject is outside the scope of this book. There also is some evidence that plants can be hardened or acclimated to high temperature, and this is discussed in Part IV.

5.6. Water Use Efficiency

The "efficiency" with which water is used refers in general to the amount of water used per unit of plant material produced. Like the term itself, however, this has been expressed in various ways. At one time "water requirement" designated the amount of water transpired per unit of dry matter produced by a crop. Later this term was replaced by "transpiration ratio," since there is no specific amount of water *required* to grow a crop. For example, water requirement or transpiration ratio for corn varied from 250 to 400 and for alfalfa from 660 to over 1000, over a period of 7 years at Akron, Colorado (8, p. 499). These data were based on transpiration rates of plants grown in containers.

In recent years the term "water use efficiency" (WUE) has come into general use, but it is employed in at least two ways. Physiologists sometimes calculate WUE in units such as mg CO_2/g H_2O, or occasionally as mol CO_2/mol H_2O. This is the ratio of carbon fixed in photosynthesis to water lost by transpiration. This use of the term is discussed in detail by Fischer and Turner (24) and it is used in this book by Nobel (Chapter 4).

Agronomists usually define *water use efficiency* in terms of the ratio of dry matter produced or crop yield, to water used in transpiration and evaporation. Thus:

$$\mathrm{WUE} = \frac{\text{dry matter or crop yield}}{\text{evapotranspiration}} \tag{1.3}$$

This places emphasis on the amount of water used per unit of economic product, such as grain, forage, fruit, or wood. It also accounts for the loss in crop production of a substantial fraction of the water by evaporation from the soil. The numerator of this equation, yield, can be greatly modified by cultural practices such as early planting, high plant density, and fertilization. These can materially increase the ratio of dry matter produced to water used by a crop, although they usually have little effect on the amount of CO_2 fixed in photosynthesis per unit of water lost by transpiration. Cultural and plant breeding programs designed to increase the ratio of dry matter produced to water used by crops are discussed by various writers in the special issue of *Agricultural Meterology* subsequently published as an edited book by Stone (28) and the book *Plant Environment and Efficient Water Use*, edited by Pierre et al. (29).

6. OBJECTIVES AND PROBLEMS

In the breeding and selection of crop plants, artificial selection has replaced natural selection, and the rate of accumulation of modifications or adaptations that result in increased yield in a particular environment can be tremendously increased. To be successful, however, plant breeders need to know what kinds of modification have adaptive value. Such concepts as drought or heat tolerance are too general to form a satisfactory basis for a breeding program. Several chapters in this book identify and evaluate some of the specific morphological and physiological adaptations that contribute to tolerance of water and heat stress. This information should be equally valuable to ecologists, crop physiologists, and plant breeders. For example, the relative importance of morphological adaptations such as deep, extensively branched roots and thick cuticle compared to the physiological adaptations such as responsive stomata, regulation of osmotic potential, protoplasmic tolerance of dehydration, and C_4 carbon metabolism, need to be evaluated so that the information can be used by plant breeders in crop improvement programs and by ecologists in explaining the distribution of natural vegetation.

Because of the complexity of these problems, we may need to reconsider our research methods. For example, in controlled environment research we need to develop water stress more slowly, in the same manner as it develops in the field (17). We also need to apply stress at various stages of development, since the effects are often different when plants are stressed in the vegetative stage and in the reproductive stage. Furthermore we need to consider possible differences in behavior between individual plants in a controlled environment and plants in a crop or community out of doors. We also should make more measurements of physiological processes, chemical composition, and morphological development. Growth analysis seems desirable to learn how the growth of the various organs is modified. Such large-scale research requires a team effort.

More interdisciplinary research is necessary at every step, from identifying the problems, through research on them, to application of the results of the research to explaining plant distribution and increasing crop production. The problems of adaptation are too broad for solution by practitioners of any one discipline. Usually scientists with field experience, such as ecologists and agronomists, are required to recognize the problems at the environmental level, but physiologists can then assist in identifying and solving them at the process level. Finally ecologists, agronomists, and physiologists can join with plant breeders in finding solutions at the whole plant and crop level.

I hope that this book will aid the reader to see more clearly the kinds of problems that control the distribution of natural vegetation and the yield of crops in various climates and will show how interdisciplinary research can expedite the solution of some of them.

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